

Systematic review and molecular phylogenetic relationships of the direct developing Malagasy anurans of the *Mantidactylus asper* group (Amphibia, Mantellidae)

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The taxonomy and distribution of Malagasy frogs of the *Mantidactylus asper* group (included in the subgenus *Gephyromantis*) is revised. The group is considered to include *Mantidactylus asper*, *M. spinifer*, *M. luteus*, *M. plicifer*, *M. sculpturatus* (which is resurrected from the synonymy of *M. luteus*) and a new species described herein. Lectotypes are designated for *Rana aspera* Boulenger, 1882 (*Mantidactylus asper*), *Mantidactylus ceratophrys* Ahl, 1929 (junior synonym of *M. asper*) and *Rana plicifera* Boulenger, 1882 (*Mantidactylus plicifer*). *M. asper* and *M. spinifer* are characterized, among other features, by a distinct black-brown contrasted ventral pattern, presence of an outer metatarsal tubercle, and a moderate amount of webbing. They are apparently allopatrically distributed, *M. spinifer* occurring in south-eastern Madagascar and *M. asper* inhabiting eastern and north-eastern rainforests. *M. luteus*, *M. plicifer* and *M. sculpturatus* have a largely uniform light venter, lack the outer metatarsal tubercle and have more extended webbing. A reliable distinction of these three species is only possible in adult males, and is based on differences in femoral gland size and advertisement calls. *M. luteus* is mainly distributed in lowlands along the Malagasy east coast, while *M. sculpturatus* appears to be restricted to mid-altitudes. *M. plicifer* has been found sympatrically with *M. sculpturatus* and *M. luteus*, and is known from the south-east. The new species described herein shares characters with *M. asper* and *M. spinifer* (presence of an outer metatarsal tubercle) and with *M. luteus*, *M. plicifer* and *M. sculpturatus* (uniform venter, extended webbing). It is only known from Montagne d'Ambre in far northern Madagascar.

A molecular phylogenetic analysis based on partial sequences of the mitochondrial 16S rRNA gene supported monophyly of the *M. granulosus* group and of the *M. pseudoasper* group in the subgenus *Phylacomantis*, and of a clade containing *M. luteus*, *M. plicifer* and *M. sculpturatus*. In contrast, the *M. asper* group and the subgenus *Gephyromantis* as a whole appeared to be paraphyletic. The obtained trees indicated a possible evolution of the direct-developing lineage from brook breeding ancestors, and a reversal from direct development in *M. granulosus*. Although these

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aspects received no relevant bootstrap support, they constitute hypotheses of great interest for general questions on amphibian evolution and should be tested with extended data sets.

INTRODUCTION

The Malagasy genus *Mantidactylus* currently contains more than 70 species which show a large diversity in morphology and reproductive biology. DUBOIS (1992) and GLAW & VENCES (1994) divided the genus into a total of 12 subgenera, reflecting this diversity. Major characteristics of all *Mantidactylus* include the absence of nuptial pads in males (and, as far as known, of a strong mating amplexus), and the deposition of eggs outside the water in all species studied so far (BLOMMERS-SCHLÖSSLER, 1979). Most species additionally have specialized femoral glands on the ventral surface of thighs (GLAW et al., 2000), especially in males.

GLAW & VENCES (1994) distinguished three major clades within *Mantidactylus*. One group contains more or less arboreal species which mostly deposit their eggs on leaves above the water surface; their tadpoles are rather generalized (subgenera *Blommerisia*, *Guibemantis*, *Pandanusicola*, *Spinomantis*). A second group consists of brook-edge-dwelling species, the larvae of which often show specialized mouthparts (subgenera *Brygoomantis*, *Chonomantis*, *Hylotritachus*, *Mantidactylus*, *Ochthomantis*). The third assemblage contains three subgenera (*Gephyromantis*, *Laurentomantis*, *Phylacomantis*), while *Phylacomantis* males usually call along brooks and at least some species have free-swimming larval stages, calling males of most *Laurentomantis* and *Gephyromantis* do not aggregate around water bodies, and direct development without free-swimming larval stages has been demonstrated in two species, *Mantidactylus asper* and *M. eiselti* (BLOMMERS-SCHLÖSSLER, 1979; GLAW & VENCES, 1994). Due to this reproductive diversity, studies on these frogs have the potential to contribute to the understanding of the evolution of direct development and other specializations in anuran reproductive biology.

One basic pre-requisite for such studies, however, is a detailed basic knowledge on the species' taxonomy and distribution (GLAW & VENCES, 2000). Distributional data of Malagasy frogs are largely based on the monograph of BLOMMERS-SCHLÖSSLER & BLANC (1991) who, however, mostly did not recognize sibling species and gave no voucher specimens for the localities plotted on their distribution maps. Apart from type specimens from other collections, their work was based almost exclusively on the collections housed at Amsterdam and Paris.

In the present paper, we review the *Mantidactylus asper* group, a phenetic species assemblage in the subgenus *Gephyromantis*, distinguished from other *Mantidactylus* by reproduction independent from water, mainly nocturnal calling behaviour, largely separated lateral metatarsalia, and black paired subgular vocal sacs in males. We re-examined the material available to BLOMMERS-SCHLÖSSLER & BLANC (1991), and complemented this information by own field observations.

MATERIALS AND METHODS

ABBREVIATIONS AND MEASUREMENTS

Vocalizations were recorded using portable tape recorders with an external microphone (Vivanco EM 238) and were analyzed with the MEDAV sound analyzing system Spektro 3.2. The following morphological measurements were taken with a caliper to the nearest 0.1 millimeter: SVL, snout-vent length; HW, head width; HL, head length, ED, horizontal eye diameter; END, eye-nostril distance; NSD, nostril-snout tip distance; NND, nostril-nostril distance; TD, horizontal tympanum diameter; HAL, hand length; FORL, forelimb length; HIL, hindlimb length; FOL, foot length, FOTL, foot length including tarsus, IMTL and IMTH, length and height of inner metatarsal tubercle; TL1, length of first toe. Statistical analyses were carried out using SPSS for Windows, version 10. We performed Mann-Whitney *U* tests to test significance of intersexual differences in size and morphometric ratios (TD/SVL, relative tympanum diameter; IMTL/SVL and IMTH/SVL, relative size of inner metatarsal tubercle, FORL/SVL and HIL/SVL, relative length of fore- and hindlimbs), and of interspecific differences in selected morphological variables and ratios. Measurements are given as range, with mean \pm standard deviation in parentheses.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London (formerly British Museum of Natural History); MNHN, Muséum National d'Histoire Naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; MSNG, Museo Civico "G. Doria" di Storia Naturale, Genova; MTKD, Museum für Tierkunde, Dresden; TM, Transvaal Museum, Pretoria; UADBA, Université d'Antananarivo, Département de Biologie Animale; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZMA, Zoologisch Museum, Amsterdam; ZMB, Museum für Naturkunde, Berlin; ZSM, Zoologische Staatssammlung, München. The catalogue numbers of voucher specimens housed in the ZMA are given as the jar number followed by the field number of R. Blommers-Schlösser, since they bear no individual ZMA tags.

TAXONOMY

To avoid confusion by introducing working definitions (operational taxonomic units) and assigning them to specific names in a second step, we decided to anticipate our taxonomic proposals and use consistent names throughout this paper. This mainly regards (1) the recognition of the Montagne d'Ambre population previously considered as *Mantidactylus plicifer* by BLOMMERS-SCHLÖSSER & BLANC (1991) or as *M. cf. asper* by GLAW & VENCES (1994) as a new species which is described herein, (2) the re-definition of *Mantidactylus plicifer* as a

species of usually rather large body size and with large and distinct femoral glands from south-eastern Madagascar; (3) the recognition of mid-altitude eastern populations previously assigned to *M. luteus* by GLAW & VENCES (1994) as a distinct species *M. sculpturatus*. These decisions are largely corroborated by high genetic divergence levels between the species recognized, by the morphological differentiation of the new species from Montagne d'Ambre and by the morphological and bioacoustic differentiation and syntopic occurrence of *M. sculpturatus* and *M. plicifer* at Ranomafana. More detailed justifications are given in the respective *Identity* and *Diagnosis* sections below.

MORPHOLOGICAL TERMINOLOGY

Webbing formula is given according to BLOMMERS-SCHLÖSSER (1979). Femoral gland morphology is described according to GLAW et al. (2000). Most *Gephyromantis* species are characterized by a number of dermal spines, tubercles and ridges. The arrangement and degree of expression of these structures is often important for species definitions and probably also bears relevance for the assessment of phylogenetic relationships among species and subgenera in the genus *Mantidactylus*. To refer unequivocally to these structures, we here define a number of terms (fig. 1):

(1) *Inter-ocular tubercles* – On the upper surface of the head, between the eyes, a number of tubercles are present in many species. These are generally arranged symmetrically, either as one pair or as two pairs, and should not be mistaken with the unelevated black inter-ocular spots as present in *M. leucomaculatus* (*Phylacomantis*). In several *Phylacomantis* (*M. cornutus*, *M. redimitus*, *M. tandroka*, *M. tschenki*), one pair of rounded, black tubercles are generally present. On the contrary, in *M. asper*, *M. spinifer* and the new species described herein (*Gephyromantis*), the tubercles are generally not rounded but rather longitudinal and ridge-like; often, two pairs of such tubercles are present which sometimes appear to be a discontinuous anterior continuation of the inner dorsolateral ridges, and sometimes, in *M. spinifer*, these ridge-like tubercles are fused to form a symmetrical figure (fig. 1).

(2) *Inner dorsolateral ridges* – As a constant state in all species of the *M. asper* group, two largely continuous ridges start above or up to 4 mm behind the eyes and run medially onto the anterior back. Here they either continue straight dorsolaterally onto the posterior fourth of the back, or curve slightly towards the flanks and fade.

(3) *Outer dorsolateral ridges* – In all species of the *M. asper* group, a second pair of dorsolateral ridges runs laterally of the inner dorsolateral ridges. Often this second pair is not continuous and poorly defined.

(4) *Connecting dorsal ridge* – In some *M. spinifer*, at the point of maximum convergence of the inner dorsolateral ridges on the anterior dorsum, these are connected by a short transversal ridge.

(5) *Supraocular spines*. – Above the eyes, distinct dermal spines are usually present in all species of the *M. asper* group (and in several *Phylacomantis*: e.g. *M. cornutus*, *M. redimitus*, *M. tschenki*), although they can be small and indistinct in the new species described herein. In contrast to the rather rigid dorsal ridges, these spines are flexible.

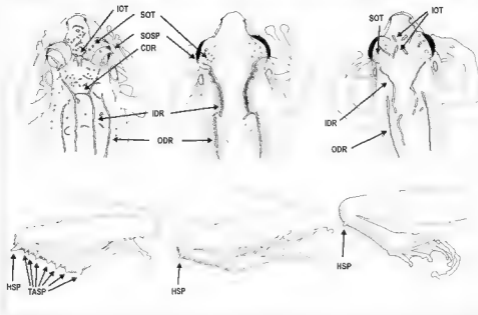


Fig. 1 - Partial dorsal views (head and anterior body and hindlimb) of three representative species of the *Mantidactylus asper* group: *Mantidactylus spinifer* (left), female MNHN 1972 1444, *M. plicifer* (center), female MNHN 1972 1431, and *M. anoholtra* (right), female MNHN 1893 245. The arrows mark dermal structures which are described in the text: CDR, connecting dorsal ridge; HSP, heel spine; IDR, inner dorsolateral ridge; IOT, inter-ocular tubercles; ODR, outer dorsolateral ridge; SOSP, suprocular spines; SOT, supraocular tubercles; TASP, tarsal spines. Not to scale.

(6) *Supraocular tubercles*. These are homologous to supraocular spines but less elevated and not pointed.

(7) *Heel spine*. A long or short spine may be present on the heel. Similar to the supraocular spines, the heel spine is a dermal, flexible structure. Beside the *M. asper* group, it is also found in several *Phyllacomantis* and in species of the genus *Boophis* (e.g., *B. madagascariensis*).

(8) *Tarsal spines*. A number of smaller dermal spines are sometimes arranged at the posterior edge of tarsus. Species with tarsal spines always bear also a distinct heel spine.

(9) *Humeral protuberance*. A well known synapomorphy of *Mantidactylus* species are the femoral glands on the ventral surface of the femur (GLAW et al., 2000). In several species of the *M. asper* group (*M. luteus*, *M. plicifer*, *M. spinifer*), we observed a prominent structure on the ventral side of the humerus, too (fig. 2). By dissection (internal view, GLAW et al., 2000), we noted that this prominence was not caused by enlargement of skeletal or muscular tissues but largely dermal, and sometimes contained a gland-like element at its most prominent part. Without further histological analyses we are unable to state whether this structure is actually a gland, and thus here refer to it as humeral protuberance. It is best visible in

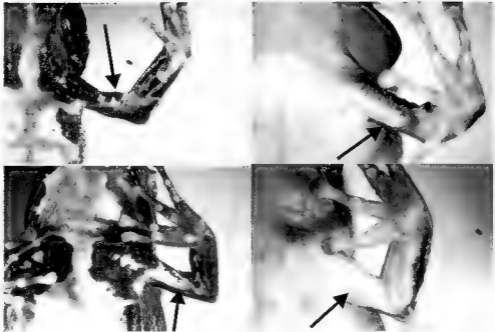


Fig. 2 - Left ventral views of a male (above, MNIIN 1972 1462) and a female (below; MNHN 1972 1443) of the forelimb of *Mantidactylus spinifer*. The arrows mark the humeral protuberances. Note also the strongly contrasted ventral pattern in both sexes. Right ventral views of a male (above MNHN 1972.1436) and a female (below MNHN 1972 1431) of the forelimb of *M. phycifer*. In this species, the humeral protuberance is very distinct in males but apparently absent in females.

Mantidactylus phycifer and *M. luteus*, where a clear sexual dimorphism exists (no protuberance recognizable in females; fig. 2). In other species, e.g. *M. spinifer*, a weakly expressed humeral protuberance appears to be present in males and females (fig. 2).

MOLECULAR AND PHYLOGENETIC METHODS

To sample data on genetic differentiation and phylogenetic relationships, we sequenced fragments of the mitochondrial 16S rRNA gene of up to 567 base pairs (bp), using primers and protocols given by VENCES et al. (2000), in species of the *M. asper* group and of related taxa. The corresponding voucher specimens and EMBL/Genbank accession numbers are *Mantidactylus asper*, UADBA-FG/MV 2000.17, AJ314802, *M. luteus*, ZFMK 66674, AF215313, *M. phycifer*, ZFMK 62306, AJ314800, *M. sculpturatus*, ZFMK 62304, AJ314799, *M. boulengeri*, ZFMK 66672, AF215318; *M. cornutus*, ZFMK 70494, AF215320, *M. cf. pseudolusper*, MSNG 49087, AJ314803, *M. malagastus*, MRSN A1991, AJ314797; *M. aff. malagastus*, MRSN A1938, AJ314796, *M. granulatus*, ZSM 645.2001, AJ314794, *M. sp. n.* (Tsaratanana; new species close to *M. grandatus*), ZSM 627.2001, AJ314795, *M. leucomaculatus*, ZFMK 59953, AJ314805, *M. cornutus*, ZSM 308.2000, AJ314798; *M. tschenki*, ZFMK 62296, AJ314806, *M. tandroka*, ZFMK 59894, AJ314803, *Boophis xerophilus* (ZFMK 66705,

AF215335) and *Mantidactylus lber* (subgenus *Gubemantis*; ZSM 491.2000, AJ314801) were used as outgroups. Sequences of the new species described below were obtained from the specimen MTKD 37424 and have the Genbank accession number AF215327.

Sequences were aligned using the CLUSTAL algorithm in SEQUENCE NAVIGATOR (Applied Biosystems); subsequently, the alignment was adjusted by eye. A total of 33 base pairs of the hypervariable region could not be reliably aligned and were excluded from further analysis. The aligned sequences were submitted to analysis using PAUP*, version 4.0 (SWOFFORD, 2001). We used MODELTEST (POSADA & CRANDALL, 1998) to estimate the model of sequence evolution for a Maximum Likelihood (ML) phylogenetic reconstruction. We additionally performed Maximum Parsimony (MP) analyses, using the heuristic search option with tree-bisection reconnection branch-swapping, and Neighbor-joining (NJ) analyses, with LogDet distances which are robust against possible variation of sequence evolution among lineages (LOCKHART et al., 1994). In the MP analyses, we coded gaps as fifth state, but also performed additional searches excluding all characters with gaps in one or more species. We used PAUP* to test for the presence of a significant phylogenetic signal by a permutation-tailed-probability (PTP) test with 100 replicates, and for homogeneity of base frequencies across sequences.

RESULTS

SPECIES ACCOUNTS

Mantidactylus asper (Boulenger, 1882)

(fig. 3a-b)

Rana aspera Boulenger, 1882 - *Name bearing type* lectotype, by present designation, BMNH 1882.3.16.80, adult male collected by W. D. Cowan, SVL 27.8 mm. *Type locality* "East Betsileo" according to original description. *Other types* paralectotypes, following present lectotype designation, BMNH 1882.3.16.81-90, same collecting data as lectotype.

Mantidactylus ceratophrys Ahl, 1929 - *Name bearing type* lectotype, by present designation, ZMB 10443, adult female, collected by J. M. Hildebrandt according to original description. *Type locality* "Betsileo" according to original description. *Other types* paralectotypes, following present lectotype designation, ZMB 10444 and 50501-50502, three adult females with same collecting data as lectotype.

Comments (1) Considering the existence of at least one new species in the *M. asper* group as described below it appears important for taxonomic stability to define single name-bearing types for all taxa in the group. Following this rationale, we here designate lectotypes for *M. asper* and its junior synonym *M. ceratophrys*. Detailed morphological measurements of these lectotypes are given in tab. 1. (2) BLOMMERS-SCHLOSSER & BLANC (1991) listed the specimens "BMNH 1882.3.16.80-82, 83-86" as syntypes of *M. asper*. The number "316" in this mention is certainly a typing error for "316". Beside BMNH 1882.3.16.80-81, all specimens of the

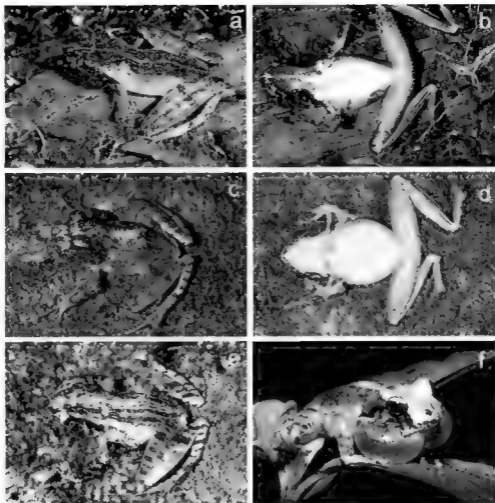


Fig. 3. Photographs of *Mantidactylus asper*, male from Ankemheny (ZI MK 60789) in dorsolateral and ventral views (a-b), of *Mantidactylus ambohitra* male holotype from Montagne d'Ambre (ZSM 1084 2001) in dorsolateral and ventral views (c-d) and of two additional specimens of *M. ambohitra* female ZI MK 57419 (e) and a calling male specimen (not collected) photographed by J. Kohler (f), both from Montagne d'Ambre

series BMNH 1882.3.16.83-90 are labeled as syntypes of the taxon in the London museum. We examined four specimens of this series which were not individually numbered. We could not locate the specimen BMNH 1882.3.16.82 in the London collection, it may have been exchanged or used for osteological examinations. It can be assumed that the series of paralectotypes (according to present lectotype designation) consists of at least nine, possibly ten specimens. — (3) BLOMERS-SILBOSSER & BLANC (1991) stated that the type of *Mantidactylus*

tylus ceratophrys Ahl, 1929 was lost. In the meantime, four original syntype specimens have been rediscovered in the ZMB collection (lectotype and paralectotypes according to present designation).

Material examined. BMNH 1882 3 16 80-81, 1882 3 16 83-86 (East Betsileo, lectotype and paralectotypes), BMNH 1925 7 2 29 (Ants.hanaka), BMNH 1928 5 9 1 (Brickaville), MNHN 1972 557-558 (Tsaratana), MNHN 1972 559-560 (Mandraka), MNHN 1972 574-576, 1972 578-583, 1972.586-591 (Tsaratana); MNHN 1972 584-585 (locality uncertain), MNHN 1973 905 (Marojejy, alt. 1300 m), MNHN 1975 313 (Marojejy), MNHN 1975.317 (no precise locality), MNHN 1975.318 (Marojejy, alt. 1300 m), MNHN 1975 319-320 (Marojejy, alt. 2000 m), MNHN 1975 321 (Mandraka); ZFMK 62236-62237, 62240 (Mantady), ZFMK 62303 (Ranomafana); ZFMK 60789 (Ankeniheny), ZMA 6867 988-990 and 6868 470 (Andasibe), ZMA 6894 36, 6895 376-383 and 6895.480-482 (Mandraka), ZMA 6897 906 (Andasibe); ZMB 50501-50502 and 10443-10444 (Betsileo, lectotype and paralectotypes of *Mantadactylus ceratophrys*); ZSM 401 2000 and UADBA-FG/MV 2000.17 (Mandraka).

Morphology and diagnosis. The following morphological description is based on the type series, and on specimens from central eastern Madagascar (Mandraka, Andasibe, Mantady, Antsihanaka, Brickaville). Specimens from these localities form a well-defined homogeneous cluster, although several characters (expression of dorsal tubercles and ridges, relative hindlimb length) are subject to considerable individual variation. Other attributed specimens are discussed in the section on distribution.

Inner dorsolateral ridges prominent, either continuous (e.g. in ZMA 6867.990) or discontinuous (e.g. in ZMA 6867.989), starting 1-3 mm behind eyes. No connecting dorsal ridge in the specimens examined by us. Outer dorsolateral ridges generally present, but often not continuous, appearing as an irregular series of short folds and tubercles. One or two pairs of distinct more or less prominent ridge-like interocular tubercles. Additional smaller tubercles and short ridges on the dorsum of most specimens. Distinct supraocular spines in all specimens, two of these being especially large. A distinct heel spine; tarsal spines generally reduced to small tubercles, sometimes not recognizable (e.g. in several specimens of the type series). Femoral glands usually visible in males, but not very distinct or prominent. Vocal sac paired subgular. No clearly recognizable humeral protuberance in either sex. Webbing in most specimens reaching slightly beyond the first subarticular tubercle of the fifth toe; webbing formula 5(0.5) to 5(0.75). One inner and two outer metacarpal tubercles, the latter in contact with each other. A large (males) or medium-sized (females) inner metatarsal tubercle and a distinct, small to medium-sized outer metatarsal tubercle.

Significant or near-significant intersexual differences were found in SVL (Mann-Whitney *U* test, $P < 0.06$), in relative length of the inner metatarsal tubercle ($P < 0.005$), and in relative tympanum diameter ($P < 0.05$), but not in relative height of the inner metatarsal tubercle or limb length. Males had larger relative tympanum sizes and longer inner metatarsal tubercles than females. Male/female size ratio was 97%.

Coloration. In preservative, dorsal coloration generally brown, with more or less symmetrical light brown or dark brown markings. In ZMA 6867 988, dark brown vertebral area enclosed between inner (anterior dorsum) and outer (posterior dorsum) dorsolateral ridges, and beige flanks and areas lateral to the ridges, the beige color starting as narrow dorsolateral bands above the eyes. Hindlimbs brown with dark brown crossbands. A thin light vertebral line in ZFMK 62236. Head laterally brown, including the lips, with some rather indistinct

dark brown markings. Ventral side white on the chest and, in females, on the throat, more cream on the posterior belly. Throat in males light brown with a distinct central white longitudinal stripe, and with black lateral color coinciding with the inflatable parts of the vocal sac. In females, indistinct but sharply delimited brown vermiculations on throat and chest. Limbs ventrally light brown, with some darker pattern at the edges.

Distribution. - Beside the specimens from central eastern Madagascar, we also assign to *M asper* rather than to *M spinifer* one subadult male from Ranomafana (ZFMK 62303; vocal sac not visible, but throat laterally already slightly black colored) based on its smaller size, ventral pattern, and expression of ridges and tubercles. The situation is more difficult for the available material from the Marojejy and Tsaratanana massifs in northern Madagascar. These specimens are larger than typical *M asper*, have more weakly expressed spines and ridges (supraocular spines reduced to tubercles in most specimens), and a very weak ventral pattern. In part, they thus remind specimens from Montagne d'Ambre which are described below as a new species. However, the low amount of webbing (at fifth toe consistently 0.75-1), as well as other characters constitute a distinct difference to that species, and support the tentative inclusion of the Tsaratanana and Marojejy populations in *M asper*. Despite low number of females in this sample (only two specimens), the inner metatarsal tubercle is significantly relatively longer in males ($P < 0.05$, tab. 2-3). Male/female size ratio is 99%.

Summarizing, the species is known from the following precise localities: (1) Tsaratanana; (2) Marojejy; (3) Antsihanaka, (4) Brickaville; (5) Mantady; (6) Andasibe, (7) Ankeniheny; (8) Mandraka; (9) Ranomafana. Except for Brickaville, which is located close to sea level at the east coast, all localities in the central east are at mid-elevations, ranging from ca. 700 to 1200 m. Marojejy specimens are catalogued as originating from an elevational range of 1300-2000 m.

BLOMMERS-SCHLÖSSLER & BLANC (1991) additionally recorded the species from Les Roussettes (Montagne d'Ambre) and Ambatofitoharanana. Specimens from the former locality are here attributed to the new species described below, while the voucher specimen from Ambatofitoharanana (MNHN 1975 315) cannot be reliably attributed to any described species (see section at the end of the species accounts).

Natural history. - Calling males were observed during the day on the ground (at Ankeniheny) and after dusk from branches about 50 cm above the ground (at Mantady and Mandraka). At Ankeniheny, they were mainly found close to a swampy brook, while they called far from water bodies at Mantady, and close to a tiny brook at Mandraka. Vocal sacs did not remain inflated between notes. Each note was one expiration.

Advertisement call. - Calls were recorded at Ankeniheny on 18 February 1994, 17 15 h, at 23.5°C air temperature. They consisted of series of single notes or series of note groups of 2-4 notes each (fig. 4). Note duration was 5-13 ms (10 ± 3 ms, $n = 8$), duration of intervals between notes was 56-80 ms (66 ± 11 ms, $n = 6$). Frequency was 1700-7700 Hz, dominant frequency 3200-4200 Hz.

Similar calls were heard after dusk on 10 February 1996 at Mantady. Only series of single notes were heard (note repetition rate 1.3-1.4 per second). Frequency was about 2000-5000 Hz, dominant frequency 3500-4500 Hz.

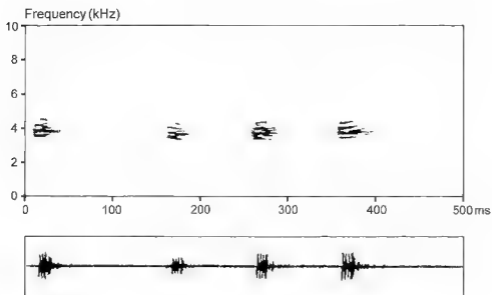


Fig. 4 ~ Sonogram and oscillogram of a call (series of four notes) of *Mantidactylus asper* from Ankenheny.

Calls from Mandraka (recorded by R. Blommers-Schlösser in December 1972 at 17 00 h) were series of note groups (up to 7 notes per group). Note duration was 13.20 ms (16 ± 2 ms, $n = 9$), duration of intervals between notes $72-80$ ms (75 ± 2 ms, $n = 7$). Note groups with 4-7 notes had a duration of $323-494$ ms (386 ± 69 ms, $n = 5$), duration of intervals between note groups was $626-733$ ms (684 ± 44 ms, $n = 4$). Frequency was $1800-6000$ Hz without recognizable dominant frequency.

Mantidactylus spinifer Blommers-Schlösser & Blanc, 1991

Mantidactylus spinifer Blommers-Schlösser & Blanc, 1991. *Name-bearing type*: holotype, by original designation, MNHN 1972 1450, adult male collected by C. P. Blanc in November-December 1971 according to MNHN catalogue. - *Type locality*: "Châines Anosyennes" according to original description, "Camp IV, Châines Anosyennes" according to MNHN catalogue. - *Parat, pes*: MNHN 1972 1440 and 1972 1470, adult female and male.

Material examined. (1) types and topotypical material: MNHN 1972 1450 (holotype, Camp IV, Châines Anosyennes), MNHN 1972 1440 (paratype, Camp IV, Châines Anosyennes), MNHN 1972 1470 (paratype, Ambana-Camp IV, Châines Anosyennes), MNHN 1972 1439, 1972 1443-1468 (Camp IV, Châines Anosyennes); (2) further material: MNHN 1972 551-554 (Ivoh, be, Marovitsika forest).

Morphology and diagnosis. Beside the three type specimens designated by BLOMMERS-SCHLÖSSER & BLANC (1991), nine males, thirteen females and four juveniles from the same

series and general locality were available. Considering this material, the following updated description of *M. spmifer* (based on the topotypic material only) can be provided. Identity of other specimens is discussed in the section on distribution.

Inner dorsolateral ridges prominent, starting 0-2 mm behind the eye. Dorsal connecting ridge present in some specimens and completely absent in others. Outer dorsolateral ridges generally present, but mostly not continuous and poorly defined, often appearing as an irregular series of short folds and tubercles. One pair of distinct and very prominent ridge-like interocular tubercles, a second, less distinct anterior pair often being also visible, the two pairs sometimes fusing to a single symmetrical structure (fig. 1). A large number of additional irregular tubercles and short ridges scattered on the dorsum. Distinct supraocular spines in all specimens, two of these being especially large. A distinct heel spine and a line of 2-7 distinct tarsal spines. Males with very distinct and rather prominent femoral glands. Vocal sac paired subgular. A weakly expressed humeral protuberance in both sexes (fig. 2). Webbing in most specimens reaching distinctly beyond last subarticular tubercle of fifth toe, but not reaching toe disc, webbing formula 5(0 25) to 5(0 75). One inner and two outer metacarpal tubercles, the latter two in contact with each other. A large inner and a distinct, small to medium sized outer metatarsal tubercle.

Morphometric measurements are given in tab. 1-3. No significant sexual dimorphism was found in relative forelimb length ($P > 0.5$), but the remaining variables tested showed significant differences between sexes: females were significantly larger (mean male/female size ratio 96%, $P < 0.05$), had shorter relative hindlimbs ($P < 0.05$), and smaller relative tympanum sizes ($P < 0.01$). Relative length and height of the inner metatarsal tubercle were also distinctly smaller in females ($P < 0.001$).

Coloration. - The following description is based on preserved specimens only, as no color pictures of living specimens were available. Dorsal coloration with various tones of brown, generally arranged in longitudinal patterns. Narrow or broad brown bands sometimes arranged dorsolaterally, following the dermal ridges, on a beige or light brown dorsum (MNHN 1972 1443, 1972 1449), or dark brown central dorsum with cream-beige flanks (MNHN 1972 1458, 1972 1461). In most specimens a rather indistinct mixture of dark and light brown.

All specimens ventrally with a very distinct coloration, the dark flank color reaching onto the posterior venter and ending abruptly, without any fading, bordering onto the ventral color which (in preservative) is bright white (fig. 2). Males with a brownish throat (laterally black, corresponding to the inflatable parts of the vocal sac) with a more or less distinct median white stripe. Females with a white throat and a brown border along the lower lip. Limbs ventrally more or less distinctly marbled with dark brown and white. This conspicuous ventral color pattern is already visible in juveniles (MNHN 1972.1452, 1972.1466-1468) of 14-18 mm SVL.

Distribution. Beside the specimens from the type locality Chaînes Anosyennes, BLUMMERS-SCHLOSSER & BLANC (1991) included three additional localities of *M. spmifer* in their distribution map: Marojejy, Marovitsika and Andringitra. The MNHN vouchers from Marojejy were herein assigned to *M. asper* and we did not locate vouchers from Andringitra assignable to the species. However, a series from the Marovitsika forest (Pic d'Ivohibe) could be included

Table 1. Morphometric measurements (all in mm) of name-bearing types in the *Mantodactylus asper* group. For abbreviation of measured variables, see *Materials and methods*; other abbreviations used are: M (male), F (female), RHL (relativ hindlamb length: gives the posture reached by the tibrotarsal articulation when the hindlamb is adpressed along the body).

Taxon	<i>Rana aspera</i> Boisenger, 1882	<i>Mantodactylus</i> <i>cecropioides</i> Ahlf, 1929	<i>Mantodactylus</i> <i>spandensis</i> Boisenger-Schöbner & Blasch, 1991	<i>Mantodactylus</i> <i>ambrosius</i> n. sp.	<i>Rana plicifera</i> Boisenger, 1882	<i>Mantodactylus</i> <i>scapulivatus</i> Ahlf, 1929
Status	Leotype	Leotype	Holotype	Holotype	Leotype	Holotype
Number*	BMNH 1882 1 16.80	ZMR 10043	MNH 1921 1450	ZSM 1054 2001	BMNH 182 3 16.58	ZMB 305 5
Sex	M	F	M	M	M	F
SVL	27.3	30	35.1	35.8	38.8	37.5
HW	9.2	9.2	12.2	13.5	13.1	13.8
HL	10.4	10.7	13.2	13.8	13.7	15
TD	2.4	2.4	2.6	3.1	2.7	2.6
ED	3.6	3.7	4.2	4.6	4.7	5.0
FND	2.9	3.2	3.4	3.3	3.4	3.4
NSD	9	2.0	2.1	2.0	2.4	2.2
NND	2.5	2.8	2.7	2.9	4.0	3.7
FORL	17.7	9.2	22.8	22.8	22.3	23.6
HAL	8.8	9.0	13	1.1	0	1.8
HIL	4.8	5.3	65.8	69.8	68.3	74.2
FOTL	21.3	25.4	29.4	29.9	30.0	33.0
FOL	15.4	16.3	20.2	21.3	19.5	2.8
IMTL	1	13	1.7	1.4	1.9	4
IMTW	1.0	0.9	1.1	0.9	4	0.8
Tf I	2.3	3.2	3.8	4.1	3.4	-
FGI	-	-	5.5	-	8.1	-
FGW	-	-	2.2	-	3.5	-
RHL	beyond snout tip	rostr.	widely beyond snout tip	widely beyond snout tip	beyond snout tip	beyond snout tip

Table 2. Morphometric measurements (all in mm) of male specimens of species in the *Mantodactylus asper* group. Abbreviations as given in *Materials and methods* and in caption to tab. 1. The measurements of *M. asper* are given separately for populations from north-eastern (NE), Iarantana (I), Marojejy (M) and central eastern (CE) Madagascar; n is the number of measured specimens. Measurements are given as mean ± standard deviation (range in parentheses). Relative hindlamb length (RHL), as coded as follows: when adpressed along body, the tibrotarsal articulation reaches (1) the rostr., (2) the snout tip, (3) beyond the snout tip or (4) widely beyond the snout tip.

Species	<i>M. asper</i> (CE)	<i>M. asper</i> (NE)	<i>M. asper</i> (I)	<i>M. ambrosius</i>	<i>M. luteus</i>	<i>M. plicifera</i>	<i>M. scapulivatus</i>
n	14	19	11	5	12	12	4
SVL	28.3 ± 0.9 (26.8-30.2)	32.8 ± 1.6 (30.8-35.5)	34.1 ± 1.0 (32.5-35.4)	35.9 ± 1.2 (34.0-37.2)	39.0 ± 2.2 (35.7-42.0)	45.0 ± 2.5 (40.8-48.3)	40.3 ± 2.4 (37.9-43.0)
HW	9.3 ± 0.4 (8.7-10.0)	11.9 ± 0.6 (10.9-13.3)	11.5 ± 0.5 (11.0-12.5)	12.7 ± 0.7 (11.5-13.3)	14.1 ± 0.7 (12.2-15.2)	16.4 ± 1.1 (13.1-17.4)	14.7 ± 0.5 (14.0-15.4)
HL	10.6 ± 0.4 (9.9-11.4)	12.8 ± 0.6 (11.7-13.7)	12.9 ± 0.5 (12.7-13.9)	13.4 ± 0.4 (12.8-13.8)	16.0 ± 0.7 (14.6-17.1)	17.7 ± 1.4 (13.7-19.3)	16.3 ± 1.2 (14.6-17.2)
TD	2.3 ± 0.2 (2.0-2.8)	2.9 ± 0.3 (2.4-3.3)	2.7 ± 0.1 (2.5-2.9)	2.7 ± 0.3 (2.4-3.1)	2.8 ± 0.2 (2.5-3.1)	2.7 ± 0.2 (2.4-2.9)	3.2 ± 0.3 (2.7-3.5)
ED	3.4 ± 0.2 (3.0-3.7)	3.8 ± 0.2 (3.3-4.3)	4.0 ± 0.2 (3.8-4.3)	4.2 ± 0.4 (3.5-4.6)	4.8 ± 0.3 (4.6-5.2)	5.2 ± 0.3 (4.7-5.6)	5.0 ± 0.3 (4.6-5.3)
FND	3.0 ± 0.2 (2.6-3.3)	3.4 ± 0.2 (3.1-3.6)	3.5 ± 0.2 (3.2-4.0)	3.3 ± 0.2 (2.9-3.7)	4.2 ± 0.3 (3.7-4.6)	4.5 ± 0.4 (3.9-4.9)	4.5 ± 0.2 (4.2-4.7)
NSD	1.8 ± 0.2 (1.5-2.2)	2.2 ± 0.2 (1.8-2.6)	2.4 ± 0.2 (2.2-2.6)	2 ± 0.2 (2.0-2.0)	3.4 ± 0.2 (2.0-2.7)	3.0 ± 0.2 (2.4-3.5)	2.6 ± 0.2 (2.4-3.0)
NND	2.3 ± 0.2 (1.8-2.4)	2.7 ± 0.3 (2.0-3.3)	2.5 ± 0.2 (2.3-2.7)	2.9 ± 0.3 (2.7-3.4)	3.4 ± 0.3 (2.7-3.8)	4.4 ± 0.2 (4.0-4.7)	3.8 ± 0.1 (3.7-3.8)
FORL	18.4 ± 1.3 (16.6-21.8)	23.1 ± 1.3 (20.1-25.1)	23.2 ± 1.3 (20.9-25.5)	23.8 ± 0.9 (22.7-24.6)	24.8 ± 1.0 (23.3-26.6)	27.9 ± 2.3 (22.5-31.0)	25.4 ± 1.3 (24.4-27.2)
HAL	8.9 ± 0.5 (8.0-9.7)	10.7 ± 0.5 (9.5-11.8)	1 ± 0.6 (1.0-12.4)	11.2 ± 0.4 (10.7-11.8)	11.5 ± 0.5 (10.4-12.2)	13.5 ± 0.9 (11.0-14.7)	11.9 ± 0.6 (11.3-12.4)
HIL	5.1 ± 0.2 (4.9-2.7)	63.9 ± 3.1 (58.1-69.9)	66.1 ± 3.8 (57.0-71.8)	68.2 ± 2.1 (65.0-70.0)	73.8 ± 4.1 (66.5-80.1)	85.8 ± 5.9 (80.3-91.0)	79.9 ± 3.2 (77.0-84.3)
FOTL	22.1 ± 1.1 (21.2-23.1)	28.3 ± 1.2 (26.3-30.5)	28.6 ± 1.3 (26.3-30.9)	29.3 ± 0.9 (28.0-30.5)	32.4 ± 1.8 (29.6-35.2)	37.8 ± 2.8 (30.0-40.7)	35.3 ± 1.9 (33.6-38.0)
FOL	15.6 ± 0.6 (14.5-16.8)	19.3 ± 1.1 (17.8-21.6)	19.7 ± 1.1 (17.4-20.9)	20.4 ± 0.9 (19.1-21.3)	21.4 ± 1.1 (21.9-23.7)	24.7 ± 1.6 (19.5-26.5)	23.3 ± 1.3 (22.4-25.1)
IMTL	1.3 ± 0.2 (1.1-1.7)	1.5 ± 0.2 (1.4-2.0)	1.8 ± 0.2 (1.3-2.1)	1.3 ± 0.1 (1.1-1.7)	1.8 ± 0.3 (1.3-2.3)	2.3 ± 0.2 (1.9-2.6)	1.8 ± 0.1 (1.7-2.0)
IMTW	0.8 ± 0.2 (0.5-1.1)	1.0 ± 0.3 (0.5-1.5)	1.1 ± 0.1 (1.0-1.4)	1.1 ± 0.1 (0.9-1.2)	3.1 ± 0.6 (0.9-3.1)	1.4 ± 0.2 (1.0-1.5)	1.1 ± 0.1 (1.0-1.2)
Tf I	2.8 ± 0.7 (2.3-3.2)	3.7 ± 0.4 (3.2-4.6)	3.7 ± 0.3 (3.2-4.2)	4.0 ± 0.2 (3.7-4.2)	4.2 ± 0.4 (3.5-5.0)	5.1 ± 0.6 (3.4-5.8)	4.6 ± 0.4 (4.1-5.0)
FGI	5.0 ± 0.9 (4.2-6.2)	4.9 ± 0.8 (4.5-5.7)	5.5 ± 0.4 (5.0-6.5)	5.1 ± 0.8 (4.5-5.5)	5.9 ± 0.8 (4.6-7.3)	8.4 ± 0.7 (7.5-9.0)	7.0 (n=1)
FGW	1.8 ± 0.1 (1.6-2.2)	1.8 ± 0.2 (1.6-2.0)	2.3 ± 0.3 (1.8-2.9)	2.1 ± 0.6 (1.7-2.5)	1.6 ± 0.3 (1.3-2.0)	3.2 ± 0.3 (2.5-3.7)	1.6 (n=1)
RHL	1-4	3-4	3-4	3-4	1-4	1-4	1-4

Table 3. Morphometric measurements (± 1 in mm) of female specimens of species in the *Mantidactylus asper* group. Abbreviations as given in *Materials and methods* and to the caption to tab. 1. The measurements of *M. asper* are given separately for populations from north-eastern (NE, Tsaratanana, Marojejy) and central, eastern (CF) Madagascar: *n* is the number of measured specimens. Measurements are given as mean ± standard deviation (range in parentheses). Relative hindlimb length (RHL) is coded as follows: when adpressed along body, the tibiotarsal articulation reaches (1) the nostril, (2) the snout tip, (3) beyond the snout tip or (4) widely beyond the snout tip.

Species	<i>M. asper</i> (CF)		<i>M. asper</i> (NE)		<i>M. spinifer</i>		<i>M. ambohitra</i>		<i>M. hoesae</i>		<i>M. pavoletti</i>	
	11	2	2	14	14	12	4	5				
SVL	39 ± 0.8 (25.2-30.3)	33.2 ± 0.1 (33.1-33.3)	35.4 ± 1.5 (32.1-38.3)	35.2 ± 0.8 (32.4-38.5)	44.1 ± 2.6 (40.8-47.0)	46.9 ± 9.4 (44.6-49.8)						
HW	9.2 ± 0.4 (8.6-10.0)	11.1 ± 0.7 (10.6-11.6)	11.5 ± 0.6 (10.7-12.3)	11.9 ± 0.9 (10.0-13.2)	16.0 ± 1.2 (15.1-17.0)	16.8 ± 0.7 (15.9-18.0)						
HL	10.9 ± 0.4 (10.2-11.5)	12.0 ± 0.6 (11.6-12.4)	13.3 ± 0.5 (12.3-14.0)	13.3 ± 0.9 (11.9-14.7)	18.2 ± 1.2 (17.3-19.9)	18.6 ± 1.0 (17.4-19.8)						
TD	2.1 ± 0.1 (2.2-4)	2.9 ± 0.2 (2.7-3.0)	2.5 ± 0.2 (2.2-4)	2.6 ± 0.7 (2.3-3)	3.1 ± 0.3 (2.8-3.4)	2.6 ± 0.2 (2.4-3.1)						
SD	1.5 ± 0.2 (1.3-3.5)	3.3 ± 0.2 (3.3-3.9)	4.1 ± 0.2 (3.7-4.3)	4.1 ± 0.3 (3.6-4)	5.5 ± 0.4 (5.0-6.5)	5.6 ± 0.4 (4.8-6.3)						
END	3.0 ± 0.2 (2.8-3.2)	3.3 ± 0.1 (3.2-3.3)	3.5 ± 0.2 (3.3-4.1)	3.3 ± 0.2 (2.8-3.6)	4.8 ± 0.2 (4.6-5.2)	4.8 ± 0.2 (4.4-5.3)						
NSD	1.9 ± 0.2 (1.5-2.3)	2.0 ± 0.5 (1.6-2.3)	2.5 ± 0.2 (2.1-2.7)	2.1 ± 0.2 (1.6-2.4)	2.6 ± 0.1 (2.7-3.2)	3.1 ± 0.3 (2.7-3.7)						
NND	2.3 ± 0.3 (1.8-2.8)	3.0 ± 0.0 (3.0-3.0)	2.5 ± 0.2 (2.3-3.0)	2.8 ± 0.2 (2.5-3.2)	3.7 ± 0.3 (3.5-3.9)	4.3 ± 0.2 (4.2-5.0)						
FORL	19.5 ± 1.0 (17.5-20.8)	22.1 ± 0.6 (22.6-23.3)	24.1 ± 0.9 (22.5-25.3)	24.9 ± 1.4 (22.8-26.9)	27.9 ± 3.1 (25.1-31.8)	29.7 ± 2.1 (28.1-31.7)						
HAL	9.0 ± 0.5 (8.1-9.6)	10.8 ± 0.6 (10.5-11.0)	10.9 ± 0.5 (10.1-11.7)	11.5 ± 0.8 (10.2-12.6)	13.1 ± 1.1 (12.2-14.6)	14.0 ± 0.5 (12.8-14.6)						
HEL	55.6 ± 1.8 (51.6-57.3)	64.7 ± 0.6 (64.2-65.1)	66.0 ± 2.8 (60.3-69.9)	71.9 ± 3.1 (67.3-75.7)	87.6 ± 4.9 (80.4-90.9)	90.6 ± 3.9 (85.1-96.2)						
POTL	24.2 ± 1.0 (22.5-24.4)	28.1 ± 0.1 (28.0-28.2)	28.4 ± 1.0 (26.8-30.4)	31.1 ± 1.5 (28.3-33.2)	39.1 ± 1.2 (36.1-40.9)	39.8 ± 1.7 (37.5-42.7)						
FOL	15.8 ± 0.8 (14.8-17.2)	19.5 ± 0.2 (19.3-19.8)	18.7 ± 0.7 (17.5-20.0)	21.1 ± 0.8 (20.0-22.4)	25.4 ± 1.8 (22.9-27.2)	25.7 ± 1.1 (23.7-27.8)						
IMTL	1.1 ± 0.2 (0.8-1.4)	1.2 ± 0.2 (1.1-1.3)	1.4 ± 0.2 (1.2-1.5)	1.3 ± 0.2 (0.9-1.5)	1.7 ± 0.2 (1.5-1.9)	1.8 ± 0.1 (1.6-2.1)						
INTW	0.7 ± 0.2 (0.5-1.0)	0.8 ± 0.2 (0.6-0.9)	0.9 ± 0.1 (0.7-1.1)	0.7 ± 0.1 (0.5-1.0)	0.9 ± 0.1 (0.7-1.1)	1.0 ± 0.0 (0.9-1.1)						
TL1	3.6 ± 0.3 (2.5-3.5)	3.9 ± 0.3 (3.7-4.1)	3.7 ± 0.3 (3.2-4.4)	4.0 ± 0.3 (3.5-4.4)	5.0 ± 0.5 (4.1-5.6)	5.1 ± 0.4 (4.6-5.6)						
RHL	1-4	3-4	-4	1-4	3-4	3-4						

with some reservations in *M. spinifer* (MNHN 1972.551-554). It contains specimens larger than typical *M. asper*, with more distinctly expressed spines and tubercles (two tarsal spines clearly recognizable) and a more distinct ventral contrast of white and dark coloration. These character states remind those of *M. spinifer* (see below). However, the specimens are still smaller than typical representatives of the species, and the ventral pattern contrast is less expressed. We here tentatively follow their assignment to *M. spinifer* as suggested by BLOMMERS-SCHLÖSSER & BLANC (1991), but it should be kept in mind that they are intermediate between *M. spinifer* and *M. asper* in size and expression of ventral pattern contrast. The species is therefore known from (1) the Chaînes Anosyennes and (2) Ivoihobe.

Natural history and advertisement call. – Unknown.

Mantidactylus ambohitra n. sp.

(fig. 3c-f)

Holotype ZSM 1084.2001 (originally ZFMK 57418), adult male, Montagne d'Ambre, collected by Frank Glaw, Nirhy Rabibisoa and Olivier Ramilison on 14-17 March 1994.

Paratypes MNHN 1893 244-245 (two females) from Montagne d'Ambre, MNHN 1893 246 (female), 1893 248 (male), 1893 249-250 (two females), 1893.252 (female), 1893 253 (juvenile), 1991 3148 (previously 1893 246A; female), all from Mararaomby (Montagne d'Ambre), sent to the Paris museum by Alluaud and Belly in 1893, MNHN 1972.573 (female) from Montagne d'Ambre, MNHN 1975 314 (female), 1975 322 (female), 1975 325 (female), 1975.329 (female), 1975 330-331 (two males) from Les Roussettes (Montagne d'Ambre), all without precise collecting data, MTKD 37424 (male) from Montagne d'Ambre, ZFMK 57419 (female) from Montagne d'Ambre, with same collecting data as holotype, ZFMK

62204-62205 (two subadults), collected by J. Steinbrecher on 26 November 1995 at Montagne d'Ambre.

Diagnosis. A member of the genus *Mantidactylus* based on the presence of femoral glands and absence of nuptial pads in males. Assigned to the *Mantidactylus asper* group in the subgenus *Gephyromantis* based on: (1) blackish paired subgular vocal sacs in males; (2) inner and outer outer dorsolateral ridges, (3) (small) heel spines; and (4) general similarity with other species of the group. The species is in several characters intermediate between *M. asper* and *M. spinifer* on the one hand, and *M. luteus*, *M. plicifer* and *M. sculpturatus* on the other hand. It is distinguished from *M. asper* and *M. spinifer* by its largely uniformly colored ventral side, a lower amount of dermal spines, less extended webbing and less prominent dorsolateral ridges. It is distinguished from *M. luteus*, *M. plicifer* and *M. sculpturatus* by smaller body size (male SVL 34-37 mm vs. 36-48 mm), less prominent inner dorsolateral ridges, small size of heel spines and supraocular spines, presence of an outer metatarsal tubercle and occasional occurrence of interocular tubercles.

Etymology. Derived from *Ambohitra*, the Malagasy name for the Amber Mountain (Montagne d'Ambre), the type locality of the species. The name is used as invariable noun in apposition to the generic name.

Description of the holotype. – Adult male, SVL 35.8 mm (fig. 3c-d). For measurements, see tab. 1. Body slender; head slightly longer than wide, distinctly wider than body, snout rounded in dorsal and lateral views, nostrils directed laterally, slightly protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region concave; tympanum distinct, elliptical (slightly higher than wide), 67% of eye diameter; supratympanic fold very distinct, straight; tongue ovoid, distinctly bifid posteriorly, vomerine teeth distinct, in two rounded aggregations, positioned posterolateral to choanae, choanae rounded. Arms slender, subarticular tubercles single, one outer, central, and inner metacarpal tubercles present, fingers without webbing, relative length of fingers $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth, finger disks distinctly enlarged, nuptial pads absent. Hindlimbs slender, tibiotarsal articulation reaching widely beyond snout tip when hindlimb is adpressed along body, lateral metatarsalia separated by webbing, inner metatarsal tubercle distinct, outer metatarsal tubercle small but recognizable, webbing formula between toes 1(1), 2i(2), 2e(0.75), 3i(2), 3e(1), 4i(2), 4e(1.75), 5i(0.25), relative toe length $1 < 2 < 3 < 5 < 4$, third toe clearly shorter than fifth toe. Skin on the upper surface smooth, dorsolateral folds present but weakly expressed and not very prominent, inner dorsolateral folds present, starting ca. 2.5 mm behind the eyes and fading on the anterior back, outer dorsolateral folds running from ca. 4 mm posterior to the supratympanic fold to the inguinal region. Two distinct, longitudinal interocular tubercles, of same color as surrounding skin; supraocular tubercles present, supraocular spines and heel spine present but small. Ventral skin smooth on throat, slightly granular on posterior belly. Femoral glands very poorly delimited and very indistinct from both external and internal views, a patch of indistinct granules visible from internal view.

Dorsal coloration in preservative dark brown with a weakly defined vertebral region of lighter beige brown color. Posterior fifth of the dorsum and dorsal surface of the hindlegs light brown. One distinct and four indistinct dark brown crossbands on femur, one indistinct and three distinct bands on tibia, and five indistinct bands on tarsus and foot. Dorsal color of

forelimbs irregularly dark and light brown. On the flanks, the dark dorsal color fading gradually into the light ventral color. Head sides dark brown except an ill-defined light band running from the anterior eye corner to the upper lip. Ventrally cream-white with some weak symmetrical brown markings in the chest region. Throat cream-white, the inflatable lateral parts of the vocal sac black. In life, color was similar to that in preservative, the iris being light brown in its upper part, reddish brown laterally, and greyish brown in its lower part.

Variation The available specimens are largely in mediocre state of preservation, especially the MNHN specimens that were collected more than 100 years ago. Nevertheless, a relatively large variability of morphology (dorsal dermal structures) and coloration could be assessed. ZFMK 57419 (fig. 3e) has a strongly contrasted dorsal pattern of dark dorsolateral stripes on a light brown back. A further specimen (fig. 3f, not collected) had a light reddish brown head surface with a triangular posterior end, a pattern also known in *Mantidactylus luteus* (GLAW & VENCES, 1994: color plate 93) and other representatives of the genus. Another specimen (not collected) had a broad and sharply delimited median light stripe on the dorsum. The inner and outer dorsolateral ridges are always present but usually weakly expressed and often discontinuous. The inner dorsolateral ridges generally begin 2-3 mm behind the eyes. In some specimens, one or two pairs of indistinct ridge-like interocular tubercles are seen, but usually they are absent. Heel spine and supraocular spines are small, and often reduced to tubercles; tarsal spines are absent. Males have rather indistinct femoral glands. Humeral protuberances are not visible in the available material. Webbing in most specimens is rather developed, reaching almost the fifth toe disk, although it is less extended in other specimens (formula 0.75-0). The outer metatarsal tubercle is always visible though generally small. The three available juvenile paratypes already show some of the characteristics of *M. ambohitra* (e.g., not very prominent dorsolateral ridges, presence of ridge-like interocular tubercles).

Significant intersexual differences (Mann-Whitney *U* tests) were detected in relative length of fore- ($P < 0.05$) and hindlimbs ($P < 0.005$) and in relative length ($P < 0.05$) and height ($P < 0.005$) of the inner metatarsal tubercle, but not in relative tympanum diameter or SVL. Limbs are longer in females than in males, which is a rather uncommon state in Malagasy frogs; the inner metatarsal tubercle is longer and higher in males. Male/female size ratio is 102.

Further material MNHN 1893 243 (Montagne d'Ambre) is a large male specimen which reminds *Mantidactylus plicifer* by size (SVL 44.8 mm) and by its large, distinct femoral glands. The probably subadult female MNHN 1975 324 (Les-Roussettes) reminds *M. luteus* rather than *M. ambohitra*. As both specimens are in poor states of preservation, it is not possible to make a definitive statement on their identity. It is possible, however, that more than one representative of the *M. asper* group occurs at Montagne d'Ambre.

Three further specimens agree morphologically with *M. ambohitra* but are not included in the type series due to dubious or lacking information on their collecting locality. The male MNHN 1975 326 is labeled as originating from "Ifaty" but we consider it as very improbable that this refers to Ifaty in extremely arid south-western Madagascar (close to Tohara). The female MNHN 1975 332 has no locality information. Both these specimens bear numbers subsequent to small series originating from the Montagne d'Ambre region. The female MNHN 1973 896 was collected, according to the MNHN catalogue, by C. P. Blanc on 16 July 1972 at Marojejy (300 m elevation), however, its "hard" state of fixation is similar to that of

specimens from Montagne d'Ambre (e.g. MNHN 1975.332) rather than to the more flexible, obviously formalin-fixed *M. luteus* specimens from Marojejy, collected also by C. P. Blanc in July 1972 (MNHN 1973 897-902).

Distribution. – The species is so far reliably known only from (1) its type locality, Montagne d'Ambre in far northern Madagascar.

Natural history. We observed specimens during the day on the forest floor. J. Kohler (pers. comm.) observed calling males in November in the evening (20-22 h and later) during light rain, calling from bushes at the forest edge, ca. 60-150 cm above the ground. Inflated vocal sacs were paired subgular (fig. 3f).

Advertisement call. – Unknown.

***Mantidactylus luteus* Methuen & Hewitt, 1913**

(fig. 5a-b)

Mantidactylus luteus Methuen & Hewitt, 1913. *Name-bearing type* holotype, by original designation, TM 10077, adult male collected by Herschell-Chauvin. *Type locality* Fohohy – *Other types* paratypes, TM 10095-10101, two adult males, two adult females and three juveniles, and TM 10094 (exchanged with another collection according to TM catalogue).

Identity. – The type series, as examined by us in 1998, agrees morphologically with the populations attributed to *M. luteus* and inhabiting the low-elevation areas of the Malagasy east coast. This form is morphologically recognizable by: (1) rather small size, (2) distinct but rather small femoral glands in males; and (3) generally uniformly whitish venter without distinct dark chest markings. The holotype has a SVL of 41.3 mm, FGL of 6.4-6.8 mm and FGW of 1.6-1.9 mm (W. Haacke, pers. comm. in 2001), thus within the range of other male specimens herein assigned to the species (tab. 2). We will, in the following, provide a detailed morphological description of *M. luteus*, and only mention differences from this pattern in the subsequent sections on *M. plicifer* and *M. sculpturatus*.

Material examined. MNHN 1975.323 (Kianjavato), MNHN 1972.1435 (Ambana-Soavala, Chaines Anosyennes), MNHN 1972.1418 (Camp V. Chaines Anosyennes), MNHN 1973.897-902, 907, 908, 910 (Marojejy, alt. 300 m), MNHN 1973.906 (Marojejy, alt. 1300 m), MNHN 1973.909 (Marojejy, alt. 600 m), TM 10077, 10095-10101 (holotype and paratypes, Fohohy), ZFMK 47222, 47290-47291, 52711, 52713-52714 (Nosy Boraha); ZFMK 52715, 66674 (Nosy Mangabe).

Morphology. – The description provided here refers to male specimens from Marojejy (MNHN 1973.897, 1973.899-902, 1973.906-908), Nosy Mangabe (ZFMK 66674) and Nosy Boraha (ZFMK 52714) which form a morphologically homogeneous group. Morphology and attribution of other specimens is discussed in the section on distribution. Inner and outer dorsolateral ridges present and usually continuous, the inner ridge being more prominent than the outer ridge. Inner dorsolateral ridges generally beginning above the eye and running onto the central dorsum, ending in various modes, either fading or curving medially or laterally, sometimes continued as indistinct undulating structures towards the inguinal region. Outer dorsolateral ridges generally beginning in the shoulder region where the inner ridges end (fig. 1). No connecting dorsal ridge, no interocular tubercles. Supraocular tubercles and a

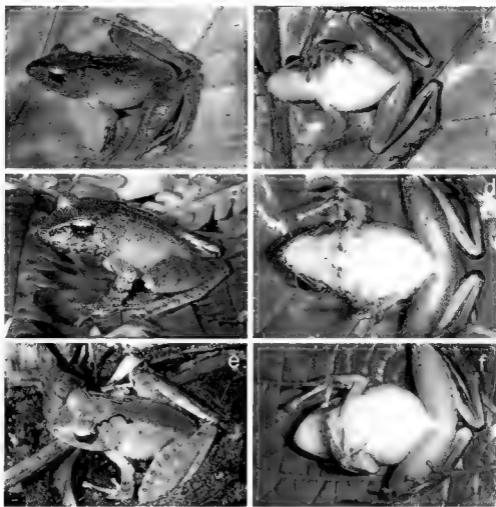


Fig. 5. Photographs of *Mantidactylus luteus*, male from Nosy Boraha, in dorsolateral and ventral views (a-b), *M. phoca*, male from Ranomafana (ZFMK 62305) in dorsolateral and ventral views (c-d), and *M. sculpturatus*, male from Andasibe (ZFMK 53688) in dorsolateral and ventral views (e-f).

few small supraocular spines present. Usually one distinct supraocular spine coinciding with the origin of the inner dorsolateral ridge. A distinct heel spine, no tarsal spines. Males with small but distinct femoral glands (see tab. 2), in MNHN 1973 899 (Marojejy), the gland on one femur, in internal view, composed of 16 granules of 0.4-0.9 mm diameter each, in ZFMK 66674 (Nosy Mangabe), of 29 granules of 0.4-0.6 mm. Vocal sac paired subgular. A strongly expressed humeral protuberance in males, lacking in females. Webbing in most specimens reaching the disc of the fifth toe, resulting in webbing formulas of 5(0) or 5(0.25). One inner and two rather weakly expressed, similarly-sized outer metacarpal tubercles, the latter two in contact with each other. A distinct inner but no outer metatarsal tubercle.

Significant intersexual differences in the whole sample attributed to *M. luteus* were found in SVL and in relative length (Mann-Whitney *U* test, $P < 0.05$) and height ($P < 0.005$) of the inner metatarsal tubercle (longer and higher in males), but not in relative tympanum diameter or relative length of limbs. Male/female size ratio is 89%.

Coloration. Dorsally generally uniformly greyish brown, sometimes with some shades and indistinct markings of lighter or darker brown. Usually with at least a partial black bordering of the inner dorsolateral ridges towards the flanks. Two further black spots often present at the origin of the outer dorsolateral ridges. Indistinct but often well-delimited crossbands on the hindlimbs (5-7 on femur, 3-7 on tibia, 4-10 on tarsus and foot). Ventral color uniformly cream, including the limbs. Only some specimens with faint brownish markings on chest and (in males) on throat. Lateral, inflatable parts of the (paired subgular) vocal sacs black.

Distribution. Beside male specimens from Marojejy, Nosy Mangabe and Nosy Boraha, we also attribute several vouchers to *M. luteus*. Two males from the Chaînes Anosyennes (MNHN 1972 1418 and 1972 1435), which were collected syntopically with *M. plicifer* (see below), differ from that species by their completely uniform chest, smaller size and smaller femoral glands (consisting of 24 granules of 0.4-0.6 mm diameter in MNHN 1972.1435). The male MNHN 1975 323 (Kianjavato) also agrees in having distinct femoral glands with 21 large granules. The females ZFMK 52711 (Nosy Boraha) and ZFMK 52715 (Nosy Mangabe) are rather large (SVL 45.0 and 47.0 mm, respectively), and would therefore agree better with *M. plicifer* by size. However, the almost uniform whitish venter of ZFMK 52711 and the very faint chest mottling of ZFMK 52715 agree with the state in *M. luteus*. As so far no records of *M. plicifer* exist for central-eastern or north-eastern Madagascar, we assign these female specimens to *M. luteus*. We attribute also the juveniles MNHN 1972 909 and 910 (Marojejy) to this species, as neither *M. plicifer* nor *M. sculpturatus* are known from this region. A further locality is Foulpointe which is based on a single voucher (ZMA 6725) which agrees with *M. luteus* in body size and femoral gland proportions according to a personal communication of F. Andreone. Summarizing, specimens attributable to *M. luteus* are from: (1) Marojejy; (2) Nosy Mangabe; (3) Nosy Boraha; (4) Foulpointe; (5) Fohohy (type locality); (6) Kianjavato; and (7) the Chaînes Anosyennes (including Ambana-Soavala and Camp V). All these localities are at low elevations along the Malagasy east coast; only one specimen (MNHN 1973 906) is catalogued as originating from 1300 m on the Marojejy massif, while the other specimens from this locality were collected at 300-600 m elevation.

BLOMMERS-SCHLÖSSER & BLANC (1991) additionally recorded the species from a number of further localities, namely Les Roussettes (Montagne d'Ambre), Ambalamarovandana, Marovitsika and Antsalova. The available Montagne d'Ambre specimens are here all referred to the new species *M. ambolitra*, although at least two of these are actually morphologically similar to *M. luteus*, and the possible occurrence of this or a similar species at Montagne d'Ambre warrants further research (see section on *M. ambolitra*). The available material from Ambalamarovandana may be attributable to *M. sculpturatus* or *M. luteus* (see below). The locality Marovitsika forest (Pic Ivohibe) is based on juvenile specimens only. The locality Antsalova (Antsingy) is corroborated by one MNHN voucher from this site catalogued as *M. luteus*. This specimen (MNHN 1975 327), however, has no dorsolateral ridges and clearly agrees in general morphology with *Mantidactylus corvus* and *M. pseudosper* (subgenus *Phylacomantis*), two morphologically similar species of which one (*M. corvus*) has been

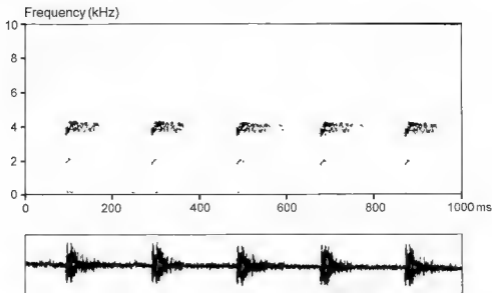


Fig. 6 Sonogram and oscillogram of part of a call (five notes of a note series) of *Mantidactylus luteus* from Marojejy.

described from western Madagascar (Isalo). Occurrence of *M. cf. pseudoasper* in the Antsingy forest is also corroborated by MSNG 49087 which was the origin of the tissue samples used for DNA analyses herein.

Natural history – Calling activity was mainly nocturnal but sometimes started before dusk. In such cases, the calls were emitted from the ground. Calling activity increased with progress of dusk, and at night specimens generally called from leaves 1–2 m above the ground. We never observed calling specimens gathering at or close to water bodies.

Advertisement call. – Calls were series of short, relatively melodious notes (fig. 6). Each note did correspond to one expiration. Between notes, the vocal sac did not remain distinctly inflated, although a slight inflation was noted when a call series was about to start. Calls from Marojejy (Camp 1) were recorded on 27 March 1994, 17–30 h, at 22°C air temperature. They contained up to 21 notes. Note duration was 22–24 ms (23 ± 1 ms, $n = 5$), duration of intervals between notes was 170–180 ms (173 ± 5 ms, $n = 4$). Note repetition rate was 5.0–5.5 ms. Calls from Nosy Boraha as described by GILW & VINCE (1992) were similar and are here re-described. They were recorded on 8 March 1991 at ca. 22°C air temperature. Note duration was 44–59 ms (51 ± 5 ms, $n = 8$), interval duration 127–236 ms (156 ± 40 ms, $n = 7$), and note repetition rate 4.3–5.0 per second.

On 28 March 1994, distress calls were emitted by a specimen from Marojejy when handled. Two calls had a duration of 1600 ms and 1663 ms. Frequency was 1650–10000 Hz.

respectively 0-10000 Hz, and showed the frequency band pattern typical for anuran distress calls.

***Mantidactylus plicifer* (Boulenger, 1882)**

(fig 5c-d)

Rana plicifera Boulenger, 1882. *Name-bearing type*, lectotype, by present designation, BMNH 1882 3 16 58, adult male collected by W D Cowan. *Type locality*: "East Betsileo" according to the original description. *Paralectotypes*: BMNH 1882 3.16 57, female and 1882 3 16.56 and 59, two subadult specimens, with same collecting data as lectotype.

Comment. The current re-definition of the species *M. plicifer* is based on characters (size and structure of femoral glands) recognizable in males only. As only one of the original syntypes of *Rana plicifera* is a male, its present designation as lectotype is necessary to reach taxonomic stability in a group of extremely similar species (*M. luteus*, *M. plicifer*, *M. sculpturatus*).

Identity – Our field observations demonstrated syntopic occurrence of a smaller and a larger *M. luteus*-like species at Ranomafana, males of the larger species reaching 44.2–44.4 mm SVL. Also in the MNHN sample from the Chaînes Anosyennes, a larger and a smaller form could be distinguished, males of the larger form ranging from 43.6 to 48.3 mm SVL. One distinctive character of the large form at both sites were its consistently large and distinct femoral glands. Based on this character, we consider the large specimens as *Mantidactylus plicifer*, fig. 7 shows that they agree with the lectotype of *Rana plicifera* in relative femoral gland size, although the type is distinctly smaller (38.8 mm SVL, see tab. 1-2). The difference both in SVL and in relative length and width of femoral glands (ratio FGL/SVL and FGW/SVL) was highly significant between *M. plicifer* and *M. luteus* ($P < 0.005$).

Material examined – BMNH 1882 3 16 56-59 (East Betsileo, lectotype and paralectotypes), MNHN 1972 1404 (Ambana-Soavala, Chaînes Anosyennes), MNHN 1972 1405, 1972 1407-1408, 1972 1410, 1972 1412-1414, 1972 1419-1422, 1972 1424-1425, 1972 1427, 1972 1429, 1972 1431 (Camp V, Chaînes Anosyennes), MNHN 1972 1436 1437 (Camp IV, Chaînes Anosyennes), ZFMK 62305-62306 (Ranomafana).

Morphology and diagnosis – Beside the larger size of most specimens as compared to *M. luteus*, the most important morphological character to identify *M. plicifer* is the large size of its femoral glands (see *Identity* section). In internal view, a gland of the lectotype contained about 45 granules. In one specimen from Ranomafana (ZFMK 62306), a gland was composed of 47 granules of 0.5–0.7 mm in diameter. In one specimen from the Chaînes Anosyennes, a gland was composed of 55 granules of 0.4–0.8 mm in diameter.

Beside this character, the morphology of *M. plicifer* is extremely similar to *M. luteus*. The differences mentioned by BLOMMERS-SCHLÖSSER & BLANC (1991) in their key to *Mantidactylus*, namely webbing (less developed in *M. plicifer*) and heel spine (only a tubercle present in *M. plicifer*) are not suited to distinguish both species. The webbing is variable in *M. plicifer*. For instance, it reaches the disk of the fifth toe in ZFMK 62306, but only inbetween the disk and the external subarticular tubercle in ZFMK 62305, resulting in webbing formulas for the fifth toe of 5(0) vs. 5(0.5). And the presence of a heel spine appears to be highly dependent on

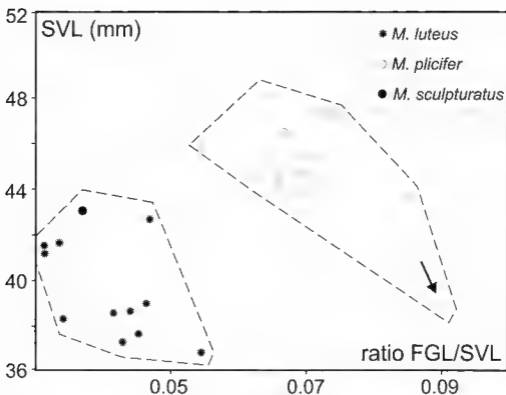


Fig. 7 Scatterplot of snout-vent length (SVL) and relative femoral gland length (ratio FGL/SVL) in *Mantidactylus luteus*, *M. plicifer* and *M. sculpturatus*. Note the clear distinction of *Mantidactylus plicifer* from the other two species by its larger femoral gland size. Most *M. plicifer* can also be distinguished by their larger SVL, the lectotype of *M. plicifer* (marked by an arrow), which in contrast is small-sized, shares with the other specimens its large femoral glands.

the state of fixation and preservation of the specimens. So, a heel spine is clearly visible in the formalin-fixed *M. plicifer* from Chaine Anosyennes, but this structure is only rudimentary and faintly recognizable in the ethanol-fixed specimens from Ranomafana. The outer metatarsal tubercle, absent in *M. luteus*, is sometimes visible as small rudiment in formalin-fixed *M. plicifer*. The pair of outer metacarpal tubercles are often indistinct in *M. plicifer* as in *M. luteus*, but when recognizable, the outermost tubercle is distinctly smaller and more elongate.

Color and pattern variation is as follows. Many specimens with a tendency of a lighter lateral coloration and a darker dorsal coloration, more or less sharply separated by the dorsolateral ridges, this contrasted pattern very distinct in a few specimens (e.g. MNHN 1972.1427) which have light brown to beige flanks and dark brown central dorsum and head surfaces, both colors sharply separated by the dorsolateral ridges. In this specimen, head also laterally beige, with a broad vertical band running from the eye to the upper lip. In some specimens, head laterally with a broad light beige band along the upper lip, bordered sharply

by a dark brown band along the canthus rostralis. Venter cream whitish, with a few brownish markings usually present in the chest region. Throat largely covered by faint brown pigment in many males (except a longitudinal light median band). Vocal sacs blackish.

Intersexual differences in SVL and relative tympanum size are close to significance (Mann-Whitney *U* test; $P < 0.07$), males being smaller and having relatively larger relative tympanum sizes than females. Highly significant differences were found in relative length and height of the inner metatarsal tubercle ($P < 0.001$; longer and higher in males), while relative limb length did not differ significantly between sexes. Mean male/female size ratio is 96 %.

Distribution Beside the unprecise type locality East Betsileo, the species is reliably known from (1) Ranomafana and (2) the Chaînes Anosyennes. BLOMMERS-SCHLÖSSER & BLANC (1991) listed six additional localities for the species: Tsaratanana, Marojejy, Ambohitantely, Mandraka, Ambalamarovandana, Marovitsika. We could not locate any voucher for the Ambohitantely locality in the MNHN or ZMA collections. The specimens from Tsaratanana, Marojejy and Mandraka, determined as *M. phycifer* by R. Blommers-Schlösser according to the MNHN catalogue, are here all referred to *M. asper* (see also GLAW & VENCES, 1994, for the Tsaratanana vouchers). The specimens from Marovitsika are juveniles that cannot be reliably determined, while those from Ambalamarovandana are here assigned to *M. sculpturatus* in a preliminary way (see below).

Natural history Calls were heard during dusk from the vegetation in rainforest. Calling males were sitting ca. 50 cm above the ground. No water bodies were observed in the surroundings.

Advertisement call Recordings were done on 2 March 1996, 18–15 h, at 23°C air temperature in the Ranomafana National Park. Single notes as well as short series of up to five notes (fig. 8) were emitted. Note duration was 121–148 ms (134 ± 10 ms, $n = 5$), duration of intervals between notes was 492–559 ms (535 ± 31 ms, $n = 4$). Since intensity faded continuously at the end of each note, measuring of note duration was difficult, and it would also be possible to consider note durations as longer (and, correspondingly, interval durations as shorter). Frequency was 1200–4000 Hz, dominant frequency 2700–3300 Hz.

***Mantidactylus sculpturatus* Ahl, 1929**

(fig. 5c-f)

Mantidactylus sculpturatus Ahl, 1929. *Name-bearing type* holotype, by monotypy, ZMB 30515. *Type locality* "Nordwest-Madagascar" according to original description (probably erroneous). *Other types*: none.

Identity. – At mid-altitude localities of eastern Madagascar, a species occurs which is extremely similar to *M. luteus* by morphology. It is, however, distinguished by its unharmonic (vs. melodious) advertisement calls, its indistinct femoral glands, and a relatively high genetic divergence (see below). We here revalidate the name *Mantidactylus sculpturatus* for this species based on the following rationale. (1) The type of *M. sculpturatus* is a female of 37.5 mm SVL; its morphology totally corresponds to species previously assigned to *M. luteus*,

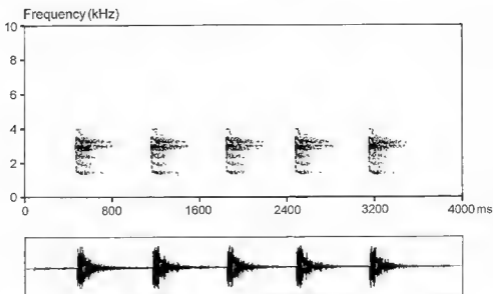


Fig 8 Sonagram and oscillogram of part of a call (five notes of a note series) of *Mantodactylus phaeifer* from Ranomafana

and its size agrees with the mid-altitude *luteus*-like species but not with the larger species *M. phaeifer*. (2) AHL (1929) described *M. sculpturatus* from a specimen that was collected by J. M. Hildebrandt, and that was reported to originate from northwestern Madagascar. However, no species close to *M. luteus* is so far known from this region, except an undescribed species from the Manongarivo Reserve collected by C. J. Raxworthy (deposited in the London museum) and by D. Rakotomalala (pers. comm.). These Manongarivo specimens, however, have distinct interocular tubercles in males and females which are absent in the type of *M. sculpturatus*. As with other anuran species collected by J. M. Hildebrandt in this region, it is probable that some labeling errors occurred either by Hildebrandt himself or when the specimens were entered in the Berlin Museum after Hildebrandt's death in Madagascar in 1881 (VINCIS & GLAW, submitted). (3) Beside localities in northwestern Madagascar, Hildebrandt collected at sites in central eastern Madagascar but apparently not at low altitudes along the east coast (BENJIE, 1998). It is therefore probable that the *M. sculpturatus* type was collected at a mid-altitude eastern locality. We are aware that these arguments do not suffice to fully clarify the identity of *M. sculpturatus*, but its present re-definition appears as most parsimonious solution and avoids the description of the mid-altitude *luteus* like form as a new species.

Note. BLOMMERS-SCHLOSSER & BÉGIN (1991) stated that the "type" of *M. sculpturatus* was lost. In the meantime, the holotype has been rediscovered in the Berlin museum.

Material examined. ZFMK 53688-53689 (Andasibe), ZFMK 62304 (Ranomafana), ZMB 30515 (holotype)

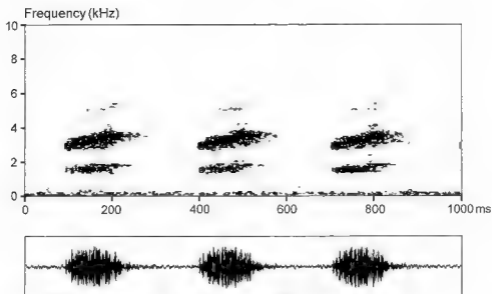


Fig. 9 Sonogram and oscillogram of a call (three notes of a note series) of *Mantidactylus sculpturatus* from Ranomafana

Morphology and diagnosis – By size and general morphology, this species is similar to *M. luteus*. Femoral glands are indistinct in most specimens, in ZFMK 62304 (Ranomafana), an adult male collected while calling and therefore in sexually mature and active state, no femoral glands at all were recognizable in external or internal view. The male ZFMK 53688 (Andasibe) had 26 scattered granules visible in internal view of a gland. These granules, however, were smaller than in *M. luteus* (0.3–0.4 mm in diameter).

In the available material, no recognizable outer metatarsal tubercle. Webbing reaching the disk of the fifth toe or slightly below, resulting in a webbing formula of 5(0)–5(0.25). A small heel spine, and two external metacarpal tubercles of approximately similar size. General coloration as in *M. luteus*, the specimen ZFMK 62304 from Ranomafana having a broad white streak along the upper lip bordered by a blackish streak running under the canthus rostralis. This specimen additionally with a curved white streak running transversally above the cloacal region. Venter uniformly light, with very faint brownish pigment on the chest in some specimens.

Distribution – The species is reliably known from (1) Andasibe, (2) Ankeniheny (no voucher specimens collected); and (3) Ranomafana.

Natural history – Calling males were observed at night, not concentrated around water bodies, 1–2 m high in the vegetation, in rainforest.

Advertisement call. – Calls from Ankeniheny were recorded on 18 December 1994, 21.45 h, at ca 22°C air temperature. They consisted of up to 22 unharmonious notes, but at the beginning

of calling activity single-note calls were common. Following several of these, note-series were successively composed of an increasing number of notes. After such a call series, calling activity was often interrupted for some minutes; one call series from Andasibe lasted 20 s and showed the following pattern: 1-1-2-3-15 (numbers referring to notes per call). However, multi note calls were emitted spontaneously as well. Note duration at Ankeniheny was 154-180 ms (168 ± 13 ms, $n = 5$), duration of intervals between notes was 126-163 ms (143 ± 18 ms, $n = 4$). Note repetition rate was 3.0-3.3 per second. Calls from Andasibe (recorded on 12 January 1992 at 22°C air temperature) were similar, with a note duration of 90-120 ms, an interval duration of 250-260 ms, and a note repetition rate of 2.8/s (GLAW & VENCES, 1994).

Calls from Ranomafana (fig. 9) were similar, too. Two analysed calls consisted of 15-17 notes and had a duration of 4463-5127 ms. Note repetition rate was 3.3-3.4/s. Note duration was 150-196 ms (173 ± 13 ms, $n = 10$), inter-note interval duration was 122-158 ms (139 ± 12 ms, $n = 10$). Frequency bands were recognizable between 1500 and 2000 Hz, 2800 and 4000 Hz, and 4800 and 5200 Hz. Dominant frequency was between 3200 and 3400 Hz.

FURTHER SPECIMENS OF UNCERTAIN ATTRIBUTION

While the specimens listed in the respective sections above could be attributed to the recognized species with a certain reliability and were used to delimit distribution patterns (fig. 10), the following juvenile specimens (and thus the localities Vondrozo, Ivohibe, Sanga Sanga forest and Tolongona) could be assigned to the complex of the three species *M. luteus*, *M. pleifer* or *M. sculpturatus*, but a specific determination was not possible. MNHN 1930.414 and MNHN 1991 3149-3150 (previously 1930 414A-B) (Vondrozo); MNHN 1972 556 (Ivohibe, Marovitsika forest), MNHN 1972.1434 (Ambana-Soavala); MNHN 1972 1406, 1972 1409, 1972.1411, 1972.1415-1417, 1972 1423, 1972 1426, 1972 1428, 1972 1430, 1972.1432-1433 (Camp V, Chaînes Anosyennes); MNHN 1972 1469 (Ambana-Camp IV, Chaînes Anosyennes); MNHN 1975.328 (Sanga Sanga forest), ZFMK 47252-47253 (Tolongona). The same applies to an adult female (MNHN 1930 413) from Fort Carnot, (SVL 42.1 mm) which is in poor state of preservation and with largely faded pattern.

A series from Ambalamarovandana (Andringitra, at 1530 m elevation, MNHN 1972 595-599) consists of two juveniles, one subadult, and two adult females with immature oocytes. By the size of the females (SVL 40.8 mm, MNHN 1972 595; 40.6 mm, MNHN 1972 596) and complete lack of dark pattern on throat and chest, they can be assigned to either *M. luteus* or *M. sculpturatus* rather than to *M. pleifer*.

Three examined specimens probably belong to the *Mantidactylus asper* group but can not be determined further at present. (1) MNHN 1975.315 (Ambatofitoharanana) is a rather large female (SVL 42.9 mm) reminding *Mantidactylus asper* and *M. ambohitra*. It has very weakly expressed, straight dorsolateral ridges and apparently no markings on the venter. The locality Ambatofitoharanana is located close to Fianarantsoa, at a rather high altitude of ca 1600 m. The specimen may represent a hitherto unknown species. (2) MNHN 1975 316 (Marojejy, no elevational information), an adult female (SVL 31.3 mm) with maturing oocytes recognizable by dissection, has two distinct pairs of ridge-like interocular tubercles, but only rudiments of dorsolateral ridges, instead, the dorsum is covered with irregular small

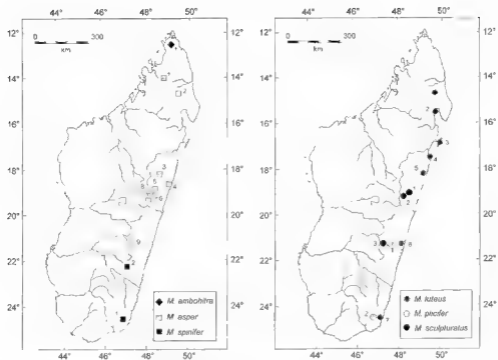


Fig. 10 Distribution maps of species in the *Mantidactylus asper* group. Locality numbers refer to those used in the text

tubercles. The venter is uniformly light except two faint symmetrical brownish markings on the chest. This individual may represent a new species of *Mantidactylus* (*Gephyromantis*), but a description does not seem justified until further collections yield also male specimens. (3) MNHN 1895 257 is a juvenile specimen in poor state of preservation that reminds *M. asper*. It is remarkable because according to the MNHN catalogue it was collected on the west coast ("Côte Ouest") However, we consider this locality information as dubious until the occurrence of the group at western localities is confirmed.

KEY TO SPECIES IN THE *MANTIDACTYLUS ASPER* GROUP

The following key allows identification of most specimens belonging to the *Mantidactylus asper* group. However, in some taxa (e.g., *M. luteus*, *M. plicifer*, *M. sculpturatus*), a reliable determination is only possible in adult males (after examination of femoral glands or advertisement calls). Considering the important variability of characters such as dorsolateral ridges within populations (e.g., of *M. asper* or *M. spinifer*), determinations based on single specimens should be always considered with caution.

- 1a. Moderately sized to large species (SVL 32-50 mm); ventrally uniformly cream-whitish, sometimes with brown mottling on chest and throat; tarsal spines and connecting dorsal ridge absent; interocular tubercles usually absent; outer metatarsal tubercle present or absent; webbing generally reaching closer to the disk of the fifth toe than to the first subarticular tubercle; webbing formula 5(0) to 5(0.5)..... 2
- 1b. Moderately sized species (SVL 27-38 mm); ventrally usually with distinct dark brown pattern (laterally delimiting a central bright white area on chest and sometimes belly; throat in males brown with a light median stripe); tarsal spines sometimes present; interocular tubercles generally present, outer metatarsal tubercle present; webbing generally closer to the first subarticular tubercle than to the disk of the fifth toe; webbing formula 5(0.5) to 5(0.75), rarely 5(0.25)..... 4
- 2a. Moderately sized species (SVL 32-39 mm); interocular tubercles sometimes present; supraocular spines small or in the form of tubercles only; dorsolateral ridges relatively irregular and indistinct; heel spine small and indistinct; outer metatarsal tubercle present, only known from far northern Madagascar (Montagne d'Ambre).....
Mantidactylus ambohitra
- 2b. Larger species (SVL 36-50 mm); interocular tubercles always absent; supraocular spines distinct, with one relatively large spine at the beginning of the inner dorsolateral ridge; inner dorsolateral ridge always distinct, heel spine distinct, outer metatarsal tubercle absent or rudimentary..... 3
- 3a. SVL 39-50 mm; femoral glands distinct, composed of 47-55 granules; calls composed of a slow series of unharmonious notes *Mantidactylus pliocifer*
- 3b. SVL 36-47 mm, femoral glands small but distinct, composed of 16-29 granules; calls composed of a rapid series of melodious notes; known from eastern lowlands
Mantidactylus luteus
- 3c. SVL 38-43 mm; femoral glands small and often indistinct or not recognizable, composed of 26 granules (if visible); calls composed of a rapid series of unharmonious notes; known from eastern mid-altitudes *Mantidactylus sculpturatus*
- 4a. Very granular dorsum with highly elevated and sharp ridges, connecting dorsal ridge often present; tarsal spines present and distinct; very distinct sharp dark brown-white contrast in the ventral pattern, extending onto the belly *Mantidactylus spinifer*
- 4b. Less granular dorsum; no connecting dorsal ridge; tarsal spines usually reduced to tubercles or absent, sharp brown-white contrast in the ventral pattern usually restricted to chest and/or throat *Mantidactylus asper*

ANALYSIS OF DNA SEQUENCES

A chi-square test did not contradict homogeneity of base frequencies across taxa ($df = 51, P > 0.9$). The PTP test resulted in a significant difference ($P = 0.01$) between the most parsimonious tree and trees generated from random permutations of the data matrix, demonstrating presence of significant phylogenetic signal. Of the total of 556 included characters, 358 were constant, 59 variable but parsimony-uninformative, and 139 variable and

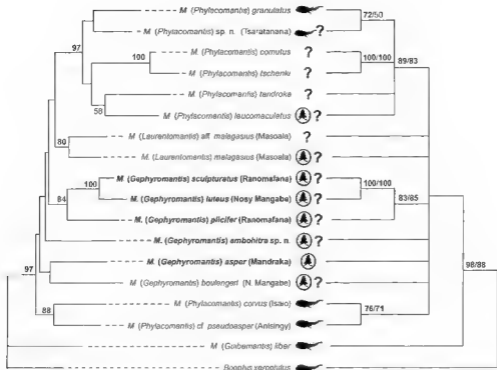


Fig. 11 Results of a Neighbor-joining (NJ, left) and a Maximum Parsimony (MP, right) analysis of 556 bp of a fragment of the mitochondrial 16S rRNA gene in 16 species of *Mantidactylus* belonging to the subgenera *Gephyromantis*, *Laurentomantis* and *Phylacomantis*. Species of the *M. asper* group are printed in bold. The MP cladogram is a strict consensus of eight equally most parsimonious trees (505 steps, consistency index 0.54, retention index 0.48). Numbers above branches are bootstrap values in percent of Neighbor joining (left) and Maximum Parsimony and Maximum Likelihood (right) analyses, respectively (2000, 2000 and 100 replicates). *Boophis xerophilus* was used as the outgroup. The symbols refer to presence of free-swimming or non feeding larvae (tadpole symbol) or direct development within the egg (egg symbol). Symbols with question marks refer to indirect evidence from calling behaviour, species which call around water bodies (brooks) may have tadpoles, while species calling independently from water probably have direct development.

parsimony-informative. MODELTEST proposed a Tamura-Nei substitution model (TrN + I + G) as best fitting the data, with a proportion of invariable sites of 0.4764, a gamma shape distribution parameter of 0.9064, and empirical base frequencies (A 0.3370, C 0.2328; G 0.1765, T 0.2536) and substitution rates (A-G: 5.3583, C-T: 8.5036, all other rates: 1). The Maximum Parsimony analysis resulted in eight equally most parsimonious trees (505 steps, consistency index 0.54, retention index 0.48). A strict consensus of these is shown in fig. 11. Most splits in the topology were unresolved, resulting in several polytomies. The following clades were resolved: (1) a lineage containing the species of the *Mantidactylus granulatus* group in the subgenus *Phylacomantis* (sensu GLAW & VENCES, 1994), (2) within the *M.*

granulatus group, one clade containing *M. granulatus* and an undescribed species from Tsaratanana, and a second clade containing *M. cornutus* and *M. tschenki*, (3) a lineage containing the two species of the subgenus *Laurentomantis* included, (4) a clade containing *M. luteus*, *M. sculpturatus* and *M. plicifer*, (5) a clade containing *M. sculpturatus* and *M. luteus*; (6) a clade with the two species of the *Mantidactylus pseudoasper* group in the subgenus *Phylacomantis*, *M. pseudoasper* and *M. corvus*.

An identical topology was obtained by a second MP analysis after exclusion of all characters with gaps in one or more taxa. The NJ analysis with LogDet distances (fig 11) and the ML analysis using the substitution model suggested by MODELTEST (not shown) supported the same clades. Both in the NJ and ML trees, the *M. pseudoasper* group was arranged basal to all other *Gephyromantis*, *Laurentomantis* and *Phylacomantis* species; sequentially, the species of *Gephyromantis* split off the phylogram, while the two *Laurentomantis* were placed as sister group of the *Mantidactylus granulatus* group.

Bootstrap analyses (FELSENSTEIN, 1985) with 2000 replicates provided rather high support for most of the clades defined above (1-6); the sole exceptions were clade 2 which was not supported by values higher than 50 % in the NJ bootstrapping, and clade 3 which received low support (51 %) in the MP bootstrapping.

Pairwise sequence divergences among species of the subgenera *Gephyromantis*, *Phylacomantis* and *Laurentomantis* ranged from 3.8 to 16.4 %. Even the lowest values (3.8 % and 4.7 % between the species pairs *M. cornutus* - *M. tschenki* and *M. luteus* - *M. sculpturatus*) were distinctly higher than values so far identified between conspecific Malagasy frog populations (up to ca. 1.5 % in *M. granulatus*; M. Vences, unpublished).

DISCUSSION

The distinctness of the three species *M. luteus*, *M. plicifer* and *M. sculpturatus* as re-defined here is well corroborated by their bioacoustic and genetic differentiation. Previous works (e.g., BLOMMERS-SCHLÖSSER & BLANC, 1991) also recognized two of these species (*M. luteus* and *M. plicifer*), but their concept of *M. plicifer* was equivocal, and in large part based on specimens attributable to *M. asper*. We observed syntopic occurrence of two species (*M. plicifer* and *M. sculpturatus*) in the field at one site (Ranomafana), and preserved material provided evidence for syntopic occurrence of *M. plicifer* and *M. luteus* at the Chaînes Anosyennes. On the other hand, the morphological differences between these species are extremely faint, and at present no reliable characters are known which could diagnose their females or juveniles. This is in agreement with the situation in almost all groups of anurans in Madagascar; the emerging picture indicates that all forms which differ bioacoustically have a high genetic differentiation and must be regarded as valid species both under evolutionary and biological species concepts. Among *M. luteus*, *M. plicifer* and *M. sculpturatus*, the lowest genetic differences are found between *M. luteus* and *M. sculpturatus*, which were reliably grouped as sister taxa by the phylogenetic analysis. The apparent allopatric distribution of these species indicates an altitudinal segregation, *M. sculpturatus* inhabiting mid elevations and *M. luteus* low-elevations along the eastern coast. This example may indicate that sibling

species that segregate along elevational gradients in Madagascar are phylogenetically younger than those which occur in close sympatry (as *M. plitsifer* *M. luteus* or *M. plitsifer* *M. sculpturatus*).

The presence of a new species, *Mantidactylus ambohitra*, at Montagne d'Ambre in far northern Madagascar has already been suspected by GLAW & VENCES (1994), who figured a specimen from this locality as "*Mantidactylus* cf. *asper*". The isolated Montagne d'Ambre rainforest shares a rather large number of species with the eastern and north-eastern rainforests which, on the contrary, are not present in the north-western (Sambirano) region (RAXWORTHY & NUSSBAUM, 1994; RASELIMANANA et al., 2000), but the taxonomy of the Ambre populations has so far not been studied in detail. Our unpublished bioacoustic and genetic data indicate substantial differentiation of the Ambre populations of at least three other species shared with the east, namely *Heterixalus betsileo*, *Mantidactylus curtus* and *Mantidactylus liber*. At least some of these populations possibly merit a status as separate species, and may have originated by allopatric speciation in the isolated rainforest patch of the Ambre massif.

As the occurrence of *Mantidactylus luteus* in Antsalova was based on a misidentification of MNHN 1975 327 (actually belonging to *M. pseudoasper* or *M. corvus*), no reliable records of any species of the *M. asper* group and of the whole subgenus *Gephyromantis* exist at present from western Madagascar. Similarly, the record of *M. granulatus* from Antsingy (BLOMMERS-SCHLÖSSLER & BLANC, 1991) is in need of confirmation as we did not find any voucher specimen in the MNHN and ZMA collections on which the distribution data of these authors were largely based. EMANUELI & JESU (1995) did not record *M. granulatus* from this area. The only records of the whole *Gephyromantis-Laurentomantis-Phylacomantis* assemblage occurring in western Madagascar refer therefore to *M. corvus* and possibly *M. pseudoasper*. This pattern correlates with reproductive modes. *M. corvus* and *M. pseudoasper* have tadpoles developing normally in brooks (though of derived morphology, see GLAW & VENCES, 1994); *Gephyromantis* have direct development (BLOMMERS-SCHLÖSSLER, 1979; GLAW & VENCES, 1994); direct development is also probable in some *Laurentomantis* (GLAW & VENCES, 1994); and the species of the *M. granulatus* group may have either direct development (e.g. *M. leucomaculatus*) or non-feeding tadpoles (*M. granulatus*), although no detailed observations have so far been published. The absence of species with direct development and similarly derived reproductive modes from western Madagascar is probably a consequence of the need of continuous humidity for the development of terrestrial nests. The seasonal environments in western Madagascar possibly do not provide the climatic continuity for successful reproduction of direct-developing in anurans or for the survival of their diminutive juveniles. This may also be the reason for the absence of cophyline microhylids of the genus *Plethodontohyla* (with non-feeding tadpoles developing in terrestrial nests) from western Madagascar.

In the molecular analyses, the subgenus *Gephyromantis* (including the *Mantidactylus asper* group) was a paraphyletic assemblage along the branch leading towards the subgenera *Laurentomantis* and partly *Phylacomantis* (the *M. granulatus* group), while another section of *Phylacomantis* was placed basal to all these taxa (*M. corvus* and *M. pseudoasper*). Relationships of *Laurentomantis* to *M. granulatus* were also obvious from the cladograms of RICHARDS et al. (2000). If this topology was confirmed by further molecular or morphological data, it would indicate (beside the obvious diphyly of *Phylacomantis*) that the assemblage of

direct-developing *Mantidactylus* species evolved from brook-breeding ancestors such as *M. corvus* and *M. pseudoasper*. If new field data confirm that *M. granulatus* has (possibly non-feeding) tadpoles rather than true direct development, the phylogenetic topology would furthermore suggest reversal of the reproductive mode (from direct development back to tadpoles) in this species. Such a (multiple) reversal has also been suggested for Neotropical hydrid frogs of the genus *Gastrotheca* (e.g., SCANLAN et al., 1980; DEL PINO & ESCOBAR, 1981; DUELLMAN & HILLIS, 1987, see also discussion in DUBOIS, 1987): in this genus, direct development appears to be the ancestral state, and montane species from the Andes are hypothesized to have re-acquired a free swimming tadpole stage through developmental arrest in the course of their evolution. However, some Andean species of direct development may have returned again to this reproductive mode (DUELLMAN & HILLIS 1987), which would indicate a high plasticity of this trait in this frog group. The testing of these hypotheses appears highly attractive to address general questions of amphibian evolution, and may qualify beside *Gastrotheca* – the *Gephyromantis-Laurentomantis-Phylacomantis* lineage as a suited model group for such studies.

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